

Dimensions and Moment Arms of the Hind- and Forelimb Muscles of Common Chimpanzees (*Pan troglodytes*)

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ABSTRACT This paper supplies quantitative data on the hind- and forelimb musculature of common chimpanzees (*Pan troglodytes*) and calculates maximum joint moments of force as a contribution to a better understanding of the differences between chimpanzee and human locomotion. We dissected three chimpanzees, and recorded muscle mass, fascicle length, and physiological cross-sectional area (PCSA). We also obtained flexion/extension moment arms of the major muscles about the limb joints. We find that in the hindlimb, chimpanzees possess longer fascicles in most muscles but smaller PCSAs than are predicted for humans of equal body mass, suggesting that the adaptive emphasis in chimpanzees is on joint mobility at the expense of tension production. In common chimpanzee bipedalism, both hips and knees are significantly more flexed than in humans, necessitating muscles capable of exerting larger moments at the joints for the same ground force. However, we find that when subject to the same stresses, chimpanzee hindlimb muscles provide far smaller moments at the joints than humans, particularly the quadriceps and plantar flexors. In contrast, all forelimb muscle masses, fascicle lengths, and PCSAs are smaller in humans than in chimpanzees, reflecting the use of the forelimbs in chimpanzee, but not human, locomotion. When subject to the same stresses, chimpanzee forelimb muscles provide larger moments at the joints than humans, presumably because of the demands on the forelimbs during locomotion. These differences in muscle architecture and function help to explain why chimpanzees are restricted in their ability to walk, and particularly to run bipedally. *Am J Phys Anthropol* 110:179–199, 1999. © 1999 Wiley-Liss, Inc.

This paper is concerned with the functional anatomy of common chimpanzees and humans and addresses the demands that locomotor repertoire imposes on anatomical features. The aim of the paper is to obtain a more detailed understanding of the origins of hominid bipedality by determining whether chimpanzees have muscle dimensions that allow them to move in a dynamically similar manner to humans, that is are the skeletal differences compensated for by

changes in joint geometry or muscle architecture? This question can be answered through

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analysis of three basic anatomical parameters. The first, the muscle physiological cross-sectional area (PCSA) reflects the number of sarcomeres in parallel and is therefore proportional to the amount of force a muscle can produce. Muscles with high PCSAs have the capacity to exert large forces (Zajac, 1992). The second parameter, the length of the fascicles (bundle of muscle fibres) reflects the number of sarcomeres in series and (in muscles whose sarcomeres have similar properties) is proportional to the maximum shortening velocity of the fascicles (i.e., the longer the fascicle, the faster is the potential velocity of shortening). In pennate muscle, the angle of pennation of the muscle fascicles with respect to the tendon also influences the capacity of the muscle to generate force. However, this effect only becomes significant for muscles with high angles of pennation ($>20^\circ$) (Zajac, 1992; Close, 1992). The requirements of different muscles to perform different functions result in design alternatives ranging from an optimal "in series" arrangement to maximise velocity and displacement, to an optimal "in parallel" arrangement to maximise force potential (Wickiewicz et al., 1983).

The moment arm of the muscle is the third anatomical parameter. It is defined as the perpendicular distance of the line of action of the muscle force to the instantaneous centre of the joint, and is equivalent to the ratio of moment over force (Spoor et al., 1990). It provides information about how a muscle transforms a linear force into an angular movement about a joint centre.

From these parameters, joint moments of force and muscle stress can be calculated. The maximum isometric stress of vertebrate skeletal muscle is approximately 300 kN m^{-2} (Wells, 1965; but see Narici et al., 1992 and James et al., 1995 for lower estimates). Maximum muscle stresses during lengthening may be as much as 75% greater than this value (Katz, 1939; Cavagna and Citterio, 1974; Flitney and Hirst, 1978). As all vertebrate striated muscle is capable of exerting the same maximum stress, it is possible to calculate the maximum moment of force that a muscle can exert about a joint. This provides information on the maximum capacity of muscles to exhibit particular joint

positions or movements [for a more detailed explanation of all these anatomical parameters see Zajac (1992)].

Substantial work has been conducted to derive accurate measures of the physiological cross-sectional area of the limb muscles in live human subjects (e.g., Narici et al., 1992 and Fukunaga et al., 1992 for the hindlimb, Kawakami et al., 1994 for the forelimb) and to calculate muscle stresses for observed ground reaction forces (Thorpe, 1997; Thorpe et al., 1998). However, much less literature is available for chimpanzees, and no study of ape muscle function has directly measured muscle PCSAs or the moment arms of the muscles about the joints [although note that Anapol and Jungers (1986) and Babcock (1994) have published data for lemurs and galagos, respectively, and Yamazaki (1985) made single estimates of the moment arms of some chimpanzee muscles]. Doran (1992a,b) and Hunt (1994) have published extensive data on the frequencies of the different locomotor modes exhibited by free ranging chimpanzees, and Hunt (1990, 1992, 1994) in particular has attempted to relate morphological characteristics of the appendicular skeleton of chimpanzees to behaviour and ecology. However, the conclusions which may be drawn from such investigations are limited by a lack of quantitative data on the forces engendered and experienced by the locomotor system of African apes other than humans, and the limits to performance capabilities these forces may set.

Considerable data now exists on the external reaction forces (see, e.g., Ishida et al., 1974; Kimura, 1985; Demes et al., 1995; Li et al., 1996) in primate bipedal and quadrupedal locomotion. However, surprisingly little work has been done on the forces and moments which the muscles are capable of exerting about the joints in the fore- and hindlimbs, although Yamazaki (1985) derived net joint moments and joint forces in bipedalism of gibbons, spider monkeys, Japanese macaques, and common chimpanzees using a computer simulation approach. He scaled moments on the basis of body mass and segment length and found that during bipedal locomotion chimpanzees exerted greater moments of force at the hip and

knee, and equal moments of force at the ankle as humans. However, these results were obtained from a chimpanzee who had been trained to walk bipedally over a period of years (personal communication to M.M.G.). The effects of training on the kinetics and kinematics of chimpanzee bipedalism are not yet documented, and some reservation must be made concerning results from trained subjects.

Some information also exist on the characteristics of muscles in primates in general. Alexander et al. (1981) studied the allometry of mammalian leg muscles and found that in general primates have longer fascicles than other more cursorial mammals. The length of the muscle fascicles directly affects the mobility of a joint, and mammals that have longer strides or a longer reach need longer fascicles. Both Alexander et al. (1981) and Rauwerdink (1991, 1993) found that the muscles of the hand and wrist tend to be larger and have longer fascicles in non-human primates than in other mammals of equal body mass. Such fascicles are necessary to allow primates to grip branches and manipulate objects with their long digits. Many of the muscles operating the fingers have very long tendons, allowing the main volume and mass of the muscles to be situated in the forearm (Ker, 1993). However, because such tendons must have a relatively small cross-sectional area, they are prone to stretch when the muscle shortens. Consequently, muscles have to shorten more, in some activities, than if the tendons were inextensible. This allows the digits to perform delicate tasks, but also means that the muscles must have longer fascicles to counteract the stretching of the tendon (Ker, 1993).

Rauwerdink (1991, 1993) further found that the fascicle lengths of the distal muscles of the hind- and forelimbs of chimpanzees were similar, a result which is to be expected in terrestrial quadrupeds/quadrumanous climbers who use hind- and forelimbs in comparable situations. However, one might predict that chimpanzee forelimbs would be less designed for force production than the hindlimbs because Kimura et al. (1979) have shown that, during quadrupedal locomotion, the forelimbs exert smaller vertical ground

reaction forces than do the hindlimbs. Kinetic studies of quadrupedalism in the common chimpanzee carried out in our laboratory (Li et al., data not shown) confirm the results of Kimura et al. Vertical forces were consistently and substantially higher in the hindlimb, and our data on sagittal forces show that the duration of acceleration of the forelimbs tends to be shorter, and the forelimb also tends to have a smaller force-time integral. Our data suggest that the hindlimb appears to be primarily responsible for driving changes in direction on broad, flat substrates. These results should not be surprising since the forelimb, used in knuckle-walking posture, is of course not well suited for applying propulsive or change-of-direction forces to the ground because of the anteroposterior shortness of the ground contact area. Interestingly Rauwerdink's (1991, 1993) analysis of the relationship between fascicle length, tendon length, and locomotor specialisation in primates also concluded that all primates have the potential to perform a variety of movements and to become specialised in any locomotor mode (Rauwerdink, 1993).

In this paper, we present quantitative anatomical data for chimpanzee hind- and forelimb anatomy, including muscle PCSAs, fascicle lengths, and moment arms. From these data, we will calculate the maximum moments that the major hind- and forelimb muscles can exert when contracting isometrically to establish whether chimpanzee muscles are capable of exerting the forces required for sustained bipedal locomotion. The paper will avoid discussing the details of individual muscles, looking instead at the overall muscular design of chimpanzees in comparison to modern humans.

MATERIALS AND METHODS

Three common chimpanzee (*Pan troglodytes*) cadavers were obtained for dissection from The North of England Zoological Society and the Zoological Society of London. These animals had died of natural causes or had been euthanased due to untreatable illness or injury. The muscles appeared to be in good condition. Information concerning the specimens is presented in Table 1. As much of the animal as possible

TABLE 1. *Subject data*

	Chimp 93	Chimp 94	Chimp 95
Sex	Male	Male	Male
Age at death	Sub adult	Adult	6 years
Mass (kg)	27.6	41.7	37
Femur length (cm)	—	—	29.0
Tibia length (cm)	—	—	24.5
Cause of death	Pulmonary problem	Euthanased after injury	Peritonitis

was dissected (allowing for injuries associated with cause of death), although only the data for leg and arm musculature are presented here. The left limbs of each chimpanzee were dissected to obtain muscle dimensions, and the right limbs were used to measure moment arms. All dissections were conducted on unfixed material which had been kept in a freezer at -20°C until required. Whilst our calculations rely heavily on data from a 6-year-old chimpanzee (chimp 95), the three individuals dissected were found to be broadly similar, and we are confident that the data obtained for Chimp 95 are representative.

Measurement of chimpanzee muscle dimensions

During dissection of each left limb, the muscles were removed systematically and weighed. Each was then cut with a sharp post-mortem knife to determine the arrangement of fibres within it. Parallel fibred muscles were cut lengthwise so that fascicle length could be measured. Pennate muscles were first cut transversely to show the positions of any internal tendons. One-half of the muscle was then cut longitudinally in such a way that muscle fibres lay in the plane of the cut and muscle fascicle lengths were measured (Alexander and Vernon, 1975). In broad muscles, where fascicle lengths are not uniform, a number of measurements were made and a mean value was taken.

The physiological cross sectional area of the muscle (A) can be obtained from

$$A = m/(\rho.l) \quad (1)$$

where m = muscle belly mass, ρ = density [$1,060 \text{ kg m}^{-3}$ (Méndez and Keys, 1960)], and l is fascicle length. For pennate muscles,

TABLE 2. *Hindlimb muscle groups*

Muscle group	Muscles
Quadriceps	Rectus femoris and the vasti
Adductors	Adductor magnus, adductor brevis, adductor longus
Hamstrings ¹	Semimembranosus, semitendinosus, biceps femoris and gracilis
Plantar flexors	Gastrocnemius, soleus and plantaris (although plantaris was only present in Chimp 93)
Deep hind flexors	Flexor hallucis longus and flexor digitorum longus

¹ Gluteus maximus is not included in the hamstring group of the chimpanzees because in apes this muscle functions primarily as a medial rotator of the thigh, rather than an extensor (Stern and Susman, 1981).

TABLE 3. *Forelimb muscle groups*

Muscle group	Muscle
Wrist flexors	Flexor carpi ulnaris, flexor carpi radialis, flexor digitorum superficialis flexor digitorum profundus
Wrist extensor	Extensor carpi ulnaris, extensor carpi radialis brevis, extensor carpi radialis longus, extensor digitorum
Elbow flexors	Biceps brachii, brachialis, brachioradialis
Elbow extensors	Triceps brachii

the PCSA is also affected by the angle of pennation (α) of the fascicles with respect to the tendon. Thus the component of force along the tendon is calculated as

$$f = F \cos \alpha \quad (2)$$

where F is the total force developed by the muscle fibres and f is the force in the tendon. However, observations conducted during the dissection showed that in chimpanzees, as in other mammals, the angle of pennation muscles is less than 30° in all fore- and hindlimb and thus $\cos \alpha$ is very close to 1. Consequently, given the accuracy of measurements on cadaveric muscle, the factor $\cos \alpha$ may be omitted, and PCSA of pennate muscle may also be calculated using Eq. (1) (Alexander, 1974; Ker et al., 1988).

To enable interspecific comparisons of muscle function, the major leg and arm muscles have been grouped into the categories shown in Table 2 and 3. These categories are based on those of Alexander (1981) to establish whether chimpanzee muscle dimensions fit the allometric equations,

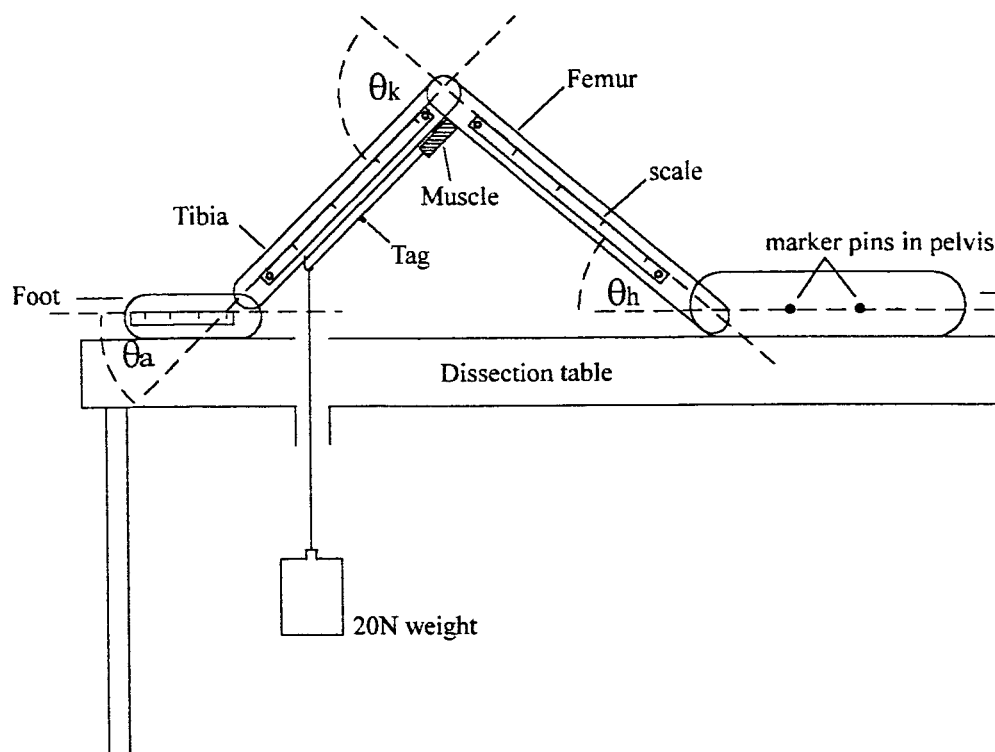


Fig. 1. Experimental set up for the measurement of moment arms, in this case the gastrocnemius lateralis at the knee. θ_h , θ_k and θ_a represent the angle of flexion of the hip, knee, and ankle respectively. For explanation of the diagram see Methods.

which were found to describe the muscle dimensions of a wide variety of mammals. However, for the purposes of this study, the adductors and hamstrings are analysed separately.

Measurement of chimpanzee moment arms

Moment arms of the major muscles at the hip, knee, ankle, shoulder, elbow, and wrist were obtained using the tendon travel method (Spoor and van Leeuwen, 1992). This technique analyses tendon displacement with respect to joint angulation, enabling calculation to be made of the "effective moment arm" (moment/force) (Spoor et al., 1990). It has the advantage that there is no need to take separate account of the geometry of the patella (Ellis et al., 1980). The method follows the principle that when a radius of a circle moves through an angle of 1 radian, any point on that radius will

have moved through an arc equal in length to the radius between that point and the centre of the circle. Thus the distance that a tendon moves while the limb moves 1 radian equals the perpendicular distance between the tendon and the joint axis, i.e., the moment arm (Brand et al., 1975).

To obtain measurements of the moment arms, photographs using slide film were taken of the tendon displacement of the muscles in situ at intervals of approximately 10° from maximum joint extension to maximum flexion, and reverse motion. Joint angles are recorded as in Figure 1. Those data for which it appeared that the joints might have been displaced beyond the normal range of motion were deleted.

For the majority of moment arm measurements, the skin was removed and the specimen was arranged on a dissection table as demonstrated in Figure 1 for the leg. Muscles were removed systematically leaving under-

lying muscles in situ so that the muscle being measured remained at its in vivo distance from the bone. For measurements, the muscle was cut leaving a stump of muscle and tendon to which a weight of 20 N was tied in order to keep the muscle-tendon unit taut (after Spoor and van Leeuwen, 1992). For the thin tendons which flex and extend the digits, a weight of only 10 N was attached using a small tendon clamp. (Many of the muscles that flex and extend the wrist also flex and extend the fingers. Thus to avoid errors due to finger movement, the fingers were kept in maximum flexion). The weight was hung down the drainage hole in the dissection table with the relevant joint positioned over the hole so that it hung uninterrupted. Millimeter scales were nailed onto the longitudinal axes of the long bones, and another scale glued to the skin of the foot in line with the centre of rotation of the ankle and the head of the metatarsals. A scale was attached to the hand in the same way. It was not possible to attach a scale to the side of the trunk, so two pins were inserted 10 cm apart in the muscle along the side of the pelvis above the superior iliac spine running in a coronal plane. Coloured tags were then glued onto the string (as shown in Figure 1) which was pulled along the millimeter scale as the joint flexed to record tendon displacement and the associated joint angle. For fan-shaped muscles, which have wide areas of origin or insertion [biceps femoris (short head) at the knee, adductor longus at the hip, latissimus dorsi, pectoralis major and teres major] pins were inserted mid-way along the origin and insertion areas, and the distance between pins measured at different joint angles. Muscle and tendon creep and string slippage were assessed on the projected slides at a later time by measuring the position of the string in relation to the bone from which it originated at 90° during forward and reverse motion. The only muscle to show a difference was gracilis at the knee which differed by 2 mm.

For moment arms at the hip, the arrangement was slightly different. The chimpanzee was laid on its side on the floor such that a line joining the two acetabula would be vertical, and its top leg being measured was

supported on boards (13.5 cm deep) to keep the leg parallel with the median plane of the body. Photographs were taken from above, and forces of approximately 20 N were applied to the muscles along the line of action as the limb was flexed.

The data were then plotted onto a graph. At any angle, the gradient of the graph of tendon displacement against joint angle represents the moment arm about the centre of rotation of that particular joint in the plane of motion (An et al., 1984). To obtain this, polynomial equations of best fit were fitted to the data, and the gradient calculated using differential calculus. This means that in cases where the best-fitting polynomial equation is linear ($y = a + bx$), the effective moment arm is a constant (b).

Calculation of maximum joint moments of force

The stress of a muscle is equal to the force it exerts per unit cross-sectional area (A), and the moment of force (M) of a muscle about a joint is the product of its force and moment arm (r). If an equal stress model is applied then the joint moment of force for a given limb position exerted when the muscle is exerting its maximum isometric stress can be calculated as:

$$M = \sigma Ar \quad (3)$$

Human muscle dimensions: hindlimb

Human muscle data were, where possible, taken from magnetic resonance imaging (MRI) studies which record muscle dimensions in healthy living subjects, thus removing the errors of using cadaveric data (Narici et al., 1992; Fukunaga et al., 1992). For muscles for which MRI data was not available, dimensions were taken from Cutts (1988) computer tomography data and Friederich and Brand's cadaveric data (1990), and scaled to the body mass of the MRI subjects. Where muscle masses are not provided (Narici et al., 1992; Friederich and Brand, 1990), they were calculated from muscle volume. Narici et al. (1992) do not provide fascicle length values. These were calculated as

$$L_f = V/A \quad (4)$$

where V = volume. The mass and PCSA for one group of muscles is the total mass and PCSA of the constituent muscles in one leg or arm. The fascicle length given for each group of muscles is a weighted harmonic mean of the lengths for the constituent muscles. This means that the mean fascicle length for the muscle group is calculated by weighting each individual muscle's fascicle length by the mass of the muscle. Thus,

$$L = \sum m_j / \sum (m_j / l_j) \quad (5)$$

where L is the fascicle length for a group of muscles of which the j th member has mass m_j and fascicles of length l_j (Alexander et al., 1981).

Human hindlimb moment arms are from Spoor and van Leeuwen (1992), Rugg et al. (1990), Visser et al. (1990), and Nemeth and Ohlsen (1985).

Human muscle dimensions: forelimb

Muscle dimensions obtained from young healthy subjects are reported in the literature for the major muscles crossing the human elbow and wrist. Kawakami et al. (1994) conducted a MRI study of the elbow muscles, and Cutts et al. (1991) reported muscle dimensions obtained from dissection of an amputated arm from a young healthy male, who had been involved in an accident. The dimensions obtained from Cutts et al. (1991) are larger than those reported in studies of cadavers (e.g., Amis et al., 1979; Edgerton et al., 1986). Moment arms of the elbow muscles are from Murray et al. (1995) and An et al. (1981). Wrist moment arms are from Armstrong and Chaffin (1978), Tolbert et al. (1985), Loren et al. (1996), and Verdan (1979).

Obtaining dimensions for the shoulder muscles proved more problematic. Some studies have provided PCSAs of these muscles obtained from cadavers (e.g., Veeger, 1991), but have not provided information for the separate heads of pectoralis major and deltoid, which perform different functions in arm flexion and extension. It is particularly difficult, both in humans and chimpanzees, to establish which fibres of the deltoid, pectoralis major, and latissimus dorsi are involved in flexion or extension, because they are large fan-shaped muscles, with wide

areas of origin. Furthermore there are no adequate data in the literature for the moment arms of the shoulder muscles in humans. [Bassett et al. (1990) do provide single measurements of the moment arms, but these were obtained when the arm was deliberately abducted and rotated into a position of instability and are therefore not relevant here.] Consequently no attempt is made in this study to compare the shoulder muscles of chimpanzees and humans, although the moment arms obtained for chimpanzee shoulder muscles are presented in Figure 3.

RESULTS

Hindlimb muscle dimensions

No qualitative differences were observed in muscle dimensions between the chimpanzee subjects, except that Chimp 94 was found to possess peroneus tertius. This muscle, present in 95% of humans (Kimura and Takahashi, 1985) but only 5% of chimpanzees (Loth, 1931), is associated with the evolution of bipedalism, since in humans it acts as a dorsiflexor and everter of the foot during the swing phase of bipedal locomotion. During bipedal walking non-human primates lacking this muscle tend to recruit peroneus longus and/or peroneus brevis in its place (Jungers et al., 1993).

In geometrically similar animals muscle mass should be proportional to body mass, fascicle length to $(\text{body mass})^{1/3}$ and cross-sectional area to $(\text{body mass})^{2/3}$. Table 4 uses these principles to scale all the subjects to the body mass of Chimp 95, and indicates that the three individuals were broadly similar to each other, suggesting that age did not have a dramatic effect on the relative muscle proportions of these animals. The dissection of Chimp 95 was the most complete dissection of the three as the cadaver had the least pre- and post-mortem damage. Furthermore, the data for this subject are likely to provide the most accurate results since the dissection benefited substantially from experience with the other two specimens. Consequently, we decided to use this animal as representative of chimpanzee anatomy rather than the mean of the three subjects. The data obtained for muscle mass, fascicle

TABLE 4. Muscle dimensions for all subjects scaled to the body mass of Chimp 95, assuming geometric similarity

	Muscle mass (kg)			Fascicle length (cm)			PCSA (cm ²)		
	Chimp 93	Chimp 94	Chimp 95	Chimp 93	Chimp 94	Chimp 95	Chimp 93	Chimp 94	Chimp 95
Quadriceps	0.47	0.52	0.55	7.9	8.6	9.2	56.3	57.7	56.0
Adductors	0.66	0.39	0.53	18.6	15.6	19.9	33.7	23.4	25.1
Hamstrings	0.52	0.72	0.42	21.0	19.5	17.7	23.3	34.9	22.4
Plantar flexors	0.30	0.28	0.29	5.8	7.0	6.6	49.2	37.8	40.5
Deep hind flexors	0.12	0.09	0.12	6.1	7.3	6.0	18.4	11.2	19.2

length, and PCSA for Chimp 95 are presented in Table 5.

Table 6 provides the dimensions of the major hindlimb muscles for hypothetical 50 kg chimpanzees and humans to enable direct comparison between muscle groups. A mass of 50 kg was chosen because it lies between the body masses of the chimpanzees and humans used in this analysis. The table shows that chimpanzee hindlimb muscle masses are generally smaller than in humans. It is unlikely that this is influenced by the fact that the chimpanzee muscle dimensions were obtained from cadaveric material, because although Chimp 95 died of an illness, Chimp 94 was euthanased immediately following an accident, suggesting that his muscle dimensions are representative of a healthy chimpanzee, and Table 4 shows that all the chimpanzees had broadly similar muscles dimensions.

Since humans have long legs and short arms, and chimpanzees short legs and long arms, it is more realistic to assess the differences in muscle mass by taking into account segment length. Table 7 shows that when muscle masses are scaled on the basis of segment length, chimpanzees possess comparatively larger muscles than do humans for all groups except for the quadriceps, which are approximately the same.

Hindlimb moment arms

Figure 2 displays the moment arms at the hip, knee and ankle for Chimp 95. Table 8 gives the equations fitted to the tendon displacement/joint angle curves from which the moment arms were derived. The degree of tendon displacement was measured for each muscle of the limb in forward and reverse motion, but no substantial differences were found for any muscle.

TABLE 5. Hindlimb muscle dimensions for Chimp 95

Muscle	Muscle mass (g)	Fascicle length (cm)	PCSA (cm ²)
Rectus femoris	93	7.8	11.3
Vastus medialis	102	9.6	10.0
Vastus lateralis	220	10	20.8
Vastus intermedius	133	9.0	13.9
Sartorius	58	30.0	1.8
Biceps femoris (long head)	85	15.7	5.1
Biceps femoris (short head)	49	10.0	4.6
Semimembranosus	67	15.8	4.0
Semitendinosus	100	26.0	3.6
Adductor longus	227	19.5	11.0
Adductor brevis	92	18.5	4.7
Adductor magnus	209	21.0	9.4
Gracilis	120	22.5	5.0
Pectineus	36	10.5	3.3
Obturatorius externus	50	6.8	6.9
Gluteus maximus	300	10.1	27.9
Gluteus medius	269	8.8	28.8
Gluteus minimus	69	6.5	10.0
Piriformis	18	6.0	2.8
Obturatorius internus	25	3.8	6.2
Quadratus femoris	18	7.7	2.2
Gemelli inferior	4	4.0	1.0
Gemelli superior	3	4.0	0.7
Soleus	128	5.5	22.0
Gastrocnemius medialis	90	8.0	10.6
Gastrocnemius lateralis	67	8.0	7.9
Plantaris	NP ¹	NP	NP
Popliteus	28	5.0	5.4
Flexor digitorum longus	41	5.3	7.2
Flexor hallucis longus	81	6.4	12.0
Tibialis posterior	65	2.5	24.6
Tibialis anterior	50	8.8	5.3
Extensor digitorum longus	29	14.0	2.0
Extensor digitorum brevis	9	4.5	2.0
Extensor hallucis longus	12	10.5	1.1
Extensor hallucis brevis	6	4.2	1.3
Peroneus longus	50	5.0	9.5
Peroneus brevis	24	6.0	3.8
Peroneus tertius	NP	NP	NP
Abductor hallucis longus	19	9.5	1.9
Flexor digitorum brevis	10	5.5	1.8
Abductor digiti minimi	8	3.0	2.6
Abductor hallucis	25	3.3	7.1
Flexor hallucis brevis	8	2.4	3.2
Adductor hallucis	30	5.0	5.6
Lumbricals	9	4.5	1.9

Terminology is from Swindler and Wood (1973).

¹ NP = muscle not present.

TABLE 6. Muscle dimensions predicted for hypothetical 50 kg chimpanzees and humans

	Muscle mass (kg)		Fascicle length (cm)		PCSA (cm ²)	
	Chimp	Human	Chimp	Human	Chimp	Human
Quadriceps	0.74	1.30	10.2	5.7	68.4	215.5
Adductors	0.71	0.70	22.0	9.2	30.6	72.2
Hamstrings	0.57	0.69	19.6	8.3	27.4	78.2
Plantar flexors	0.39	0.63	7.4	2.4	49.5	252.3
Deep hind flexors	0.16	0.07	6.6	2.9	23.5	22.0

Muscle dimensions are scaled in the same manner as for Table 2.

TABLE 7. Muscle mass scaled to (segment length)³ (kg/m³)

Muscle mass/ (segment length) ³ (kg m ⁻³)	Chimpanzee	Human
Quadriceps/(femur length) ³	22.5	24.9
Adductors/(femur length) ³	21.6	13.4
Hamstrings/(femur length) ³	17.3	13.2
Plantar flexors/(tibia length) ³	19.4	11.8
Deep hind flexors/(tibia length) ³	8.3	1.3

The quadriceps, adductors and hamstrings are scaled to (femur length)³. The plantar flexors and deep hind flexors are scaled to (tibia length)³.

Initially the moment arm of the quadriceps about the knee was measured for all four agonist muscles together. However, the dissection revealed that a number of the vastus lateralis and vastus medialis fascicles inserted into fascia on either side of the knee joint, giving them a much lower moment arm than the bulk of the muscle group. Consequently, we repeated the experiment for the entire quadriceps before separating the rectus femoris from the vasti and measuring its moment arm at the knee individually. Both moment arms are given in Figure 2. The two experiments on the entire quadriceps gave identical results. Consequently, the quadriceps moment arm in Figure 2 represents the amalgamation of both experiments.

Table 9 provides the mean mid-stance (defined as the moment at which the swinging limb passes the stance limb) moment arms for muscle groups scaled to 50 kg body mass for chimpanzees and humans. It shows that moment arms are not greatly different except that humans have larger moment arms for the quadriceps at the knee and chimpanzees have larger moment arms for the adductors at the hip.

Forelimb muscle dimensions

In general chimpanzees and humans have the same forelimb musculature, except that chimpanzees have an additional muscle, named dorsoepitrochlearis, which has been reduced to fascia in humans (Aiello and Dean, 1990). This muscle originates from the tendon of insertion of the latissimus dorsi and inserts onto the medial epicondyle of the humerus, functioning as a tensor of the arm fascia.

Table 10 gives the muscle dimensions for Chimp 95, and Table 11 provides the dimensions of the muscle groups scaled to the body mass of Chimp 95, assuming geometric similarity. The results show that the subjects were broadly similar to each other, although Chimp 94 possessed comparatively smaller elbow and wrist flexors than the other chimpanzees. Table 12 compares predicted forelimb muscle dimensions for hypothetical 50 kg chimpanzees and humans and Table 13 provides forelimb muscle masses when scaled on the basis of body mass and segment length.

Forelimb moment arms

Extensor carpi ulnaris generally inserts on the base of the fifth metacarpal (Swindler and Wood, 1973); however, in Chimp 95 it inserted on the pisiform, which is larger than in humans and situated anterior to the triquetrum rather than at the side. Consequently, it did not have a moment arm at the wrist. The deltoid of the right limb was missing, so its moment arm at the shoulder was measured as the perpendicular distance from the centre of rotation of the humerus, to an estimate of the centre of the muscle, when the arm was positioned at the side of

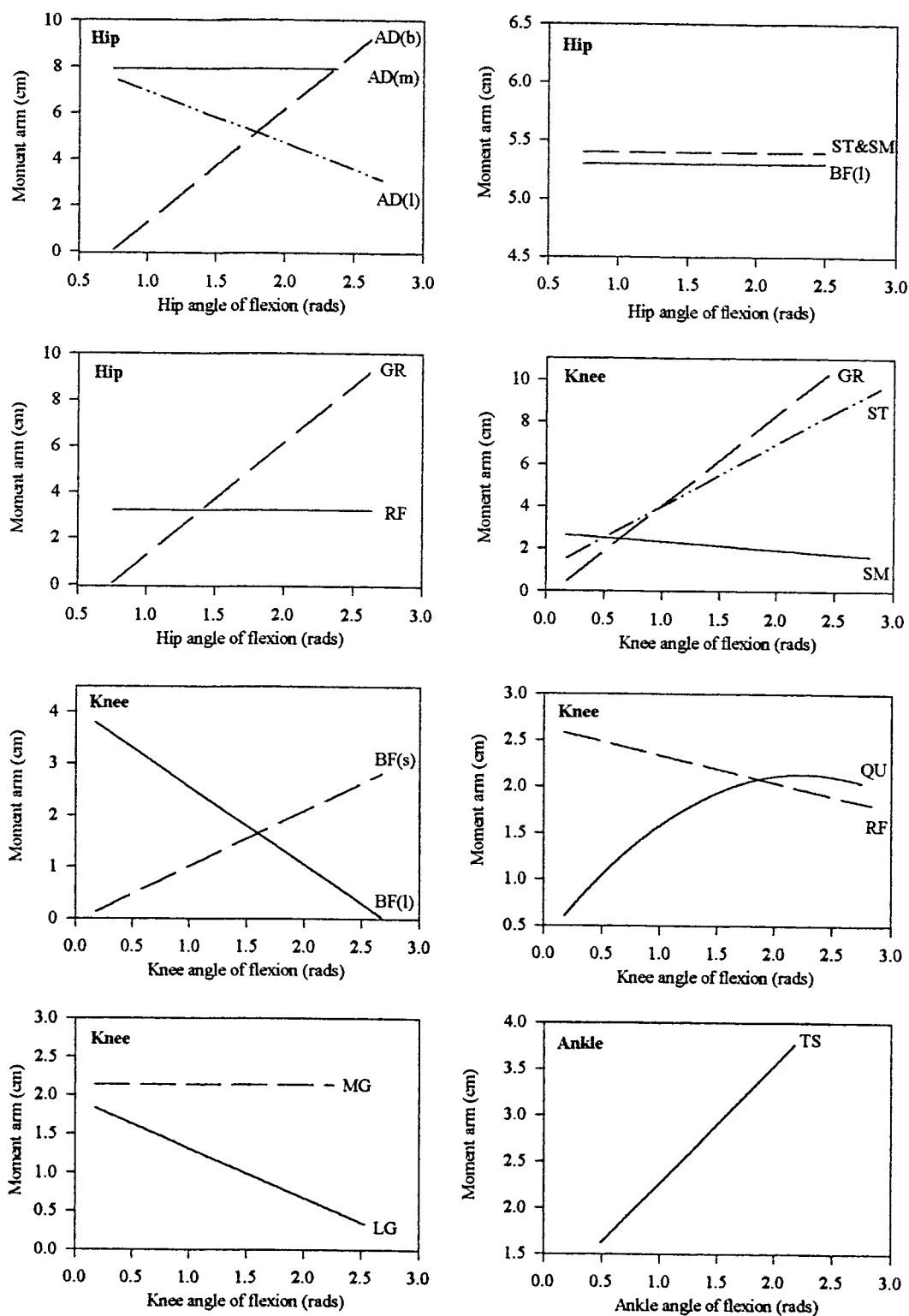


Fig. 2. Moment arms about the hip, knee and ankle. AD(l): adductor longus, AD(m): adductor magnus, AD(b): adductor brevis, BF(l): biceps femoris (long head), ST: semitendinosus, SM: semimembranosus, GR: gracilis, RF: rectus femoris, BF(s): biceps femoris (short head),

QU: total quadriceps, MG: gastrocnemius medialis, LG: gastrocnemius lateralis, TS: triceps surae. At the hip semimembranosus and semitendinosus inserted in the same place and were measured together, as were adductor brevis and gracilis.

TABLE 8. Equations of best fit and r^2 values for moment arm (cm) regressions at the hip, knee, and ankle

Muscle	Equation of best fit	r^2 value
Adductor longus (hip)	$-7.08 + 9.17x - 1.12x^2$	0.98
Adductor brevis (hip)	$7.35 + 3.63x - 2.45x^2$	0.95
Adductor magnus (hip)	$18.10 - 7.89x$	0.94
Biceps femoris long head (hip)	$13.10 - 5.30x$	0.99
Gracilis (hip)	$7.35 + 3.63x - 2.45x^2$	0.95
Rectus femoris (hip)	$-1.69 + 3.20x$	0.99
Semitendinosus (hip)	$13.3 - 5.4x$	0.99
Semimembranosus (hip)	$13.3 - 5.4x$	0.99
Biceps femoris long head (knee)	$0.76 + 4.06x - 0.75x^2$	0.97
Biceps femoris short head (knee)	$3.85 + 0.06x - 0.54x^2$	0.98
Gracilis (knee)	$0.01 - 0.26x + 2.16x^2$	0.97
Gastrocnemius lateralis (knee)	$0.27 + 1.95x - 0.32x^2$	0.97
Gastrocnemius medialis (knee)	$-0.44 + 2.14x$	0.99
Quadriceps (knee)	$4.50 - 0.33x - 0.81x^2 + 0.12x^3$	0.98
Rectus femoris (knee)	$6.33 - 2.63x + 0.15x^2$	0.99
Semimembranosus (knee)	$0.80 + 2.71x - 0.19x^2$	1.00
Semitendinosus (knee)	$0.29 + 1.04x + 1.49x^2$	1.00
Triceps surae (ankle)	$5.52 - 1.00x - 0.63x^2$	0.98

x is the joint angle (rads).

TABLE 9. Mean muscle group moment arms for the midstance posture of a bipedal stride*

	Chimpanzee			Human		
	Hip	Knee	Ankle	Hip	Knee	Ankle
Quadriceps	3.5	2.5	—	2.8	4.1	—
Adductors	6.3	—	—	1.8	—	—
Hamstrings	5.3	3.4	—	6.2	2.8	—
Plantar flexors	—	1.8	3.7	—	1.8	4.4

* Calculated for a body mass of 50 kg, assuming geometric similarity.

TABLE 10. Forelimb muscle dimensions for Chimp 95

Muscle	Muscle mass (g)	Fascicle length (cm)	PCSA (cm ²)
Deltoid	276	8.3	31.4
Latissimus dorsi	373	24.0	14.7
Infraspinatus	116	6.8	16.1
Teres major	73	14.2	4.8
Teres minor	21	6.8	2.9
Coracobrachialis	38	5.6	6.3
Biceps brachii (longus)	88	12.5	6.7
Biceps brachii (brevis)	108	15.0	6.8
Brachialis	133	9.2	13.6
Triceps brachii (long)	133 ¹	10.0	12.6 ¹
Triceps brachii (medial)	201	9.0	21.1
Dorsoepitrochlearis	43	9.5	4.3
Pronator teres	44	6.6	6.4
Flexor carpi radialis	56	7.0	7.5
Palmaris longus	8	4.7	1.7
Flexor carpi ulnaris	65	5.2	11.9
Flexor digitorum superficialis	130	6.8	18.0
Flexor digitorum profundus	176	15.4	10.8
Brachioradialis	114	17.5	6.1
Extensor carpi radialis longus	44	11.5	3.6
Extensor carpi radialis brevis	38	9.0	4.0
Extensor digitorum	48	6.0	7.6
Extensor carpi ulnaris	26	4.0	6.0
Anconeus	6	3.1	1.7
Supinator	39	3.5	10.5
Abductor pollicis longus	32 ²	4.0	7.6 ²
Extensor pollicis brevis	—	4.0	—
Extensor pollicis longus	7	4.0	1.7
Pronator quadratus	12	2.5	4.6
Flexor pollicis brevis	13	4.0	3.0
Adductor pollicis (caput transversum)	7	4.8	1.4
Adductor pollicis (caput obliquum)	4	3.8	1.0
Abductor digiti minimi	13	4.0	3.0
Lumbricals	9	10.5	0.8

Terminology is from Swindler and Wood (1973).

¹ Total of triceps brachii (long) and triceps brachii (lateral).

² Total of abductor pollicis longus and extensor pollicis brevis.

the trunk in the anatomical position. It measured 3.3 cm.

Figure 3 displays the moment arms at the shoulder, elbow, and wrist for Chimp 95, while Table 14 gives the equations fitted to the tendon displacement/joint angle curves, from which the moment arms were derived. As with the hindlimb moment arms, no substantial differences in tendon displacement were found when the limb was moved in forward and reverse motion. Table 15 provides the mean moment arms for chimpanzee and humans forelimb muscle group, scaled to 50 kg body mass. The joint angles used to calculate the mean value are limited by the available human data, so the elbow

angle is 50° flexion (0.87 rads), and the wrist is in a neutral position (i.e., 0° flexion). However, in Chimp 95, the wrist did not naturally extend as far as 0° flexion. Prior to dissection, maximum extension was 45° flexion (0.79 rads), and consequently this angle will be used for the chimpanzee moment arms at the wrist. This appears to be a condition peculiar to Chimp 95, since photographs of other chimpanzees confirm that the wrist can extend to 0° flexion. Unfortunately, it is not clear what caused the lack of mobility at this joint. Consequently, there are inaccuracies in this analysis, but it will provide relative values which will indicate

TABLE 11. Muscle dimensions for all chimps scaled to the body mass of Chimp 95 (37 kg), assuming geometric similarity

	Muscle mass (kg)			Fascicle length (cm)			PCSA (cm ²)		
	Chimp 93	Chimp 94	Chimp 95	Chimp 93	Chimp 94	Chimp 95	Chimp 93	Chimp 94	Chimp 95
Elbow flexors	0.46	0.34	0.44	15.9	12.5	12.6	27.2	25.3	33.2
Elbow extensors	0.32	0.26	0.33	9.5	8.8	9.4	31.7	27.5	33.6
Wrist flexors	0.43	0.30	0.43	8.1	7.6	8.4	50.4	37.1	48.2
Wrist extensors	0.12	0.12	0.16	7.9	5.5	6.9	14.2	20.8	21.2

TABLE 12. Muscle dimensions predicted for hypothetical 50 kg chimpanzees and humans

	Muscle mass (kg)		Fascicle length (cm)		PCSA (cm ²)	
	Chimp	Human	Chimp	Human	Chimp	Human
Elbow flexors	0.60	0.31	13.9	13.8	40.6	21.4
Elbow extensors	0.45	0.33	10.4	7.7	41.1	40.1
Wrist flexors	0.58	0.28	9.2	7.1	58.9	37.2
Wrist extensors	0.21	0.14	7.7	5.9	25.9	21.6

TABLE 13. Muscle mass scaled to (segment length)³ (kg/m³)*

Muscle mass/ (segment length) ³ (kg m ⁻³)	Chimpanzee	Human
Elbow flexors/(humerus length) ³	20.2	12.1
Elbow extensors/(humerus length) ³	15.2	12.6
Wrist flexors/(radius length) ³	24.6	23.4
Wrist extensors/(radius length) ³	9.0	11.4

*The elbow flexors and extensors are scaled to (humerus length)³. The wrist flexors and extensors are scaled to (radius length)³. Humerus length is 28.0 cm and radius length is 25.9 cm.

the general magnitude of the differences in joint moment arms between chimpanzees and humans.

DISCUSSION

Grand (1977) demonstrated that 60–80% of an animals' body mass is dedicated to the locomotor system. Yet the distribution of this mass differs between animals depending on the locomotor repertoire employed. Zihlman (1992) demonstrated that the forelimbs of humans and chimpanzees account for 9% and 16% of total body weight, respec-

tively. The chimpanzee forelimb value is the same as that of orangutans, and emphasises the importance of chimpanzee arms in hanging and climbing (Zihlman, 1992), whilst the lower value for humans reflects the comparative redundancy of the forelimb in human locomotion. The values for human and chimpanzee hindlimbs are 38% and 24% of body mass, respectively (Zihlman, 1992). The anatomical adaptations associated with ape and human locomotion are also already well documented (e.g., Schultz, 1950; Washburn, 1951), in particular the extreme forelimb mobility of apes, which allows them to locomote in highly complex arboreal environments. Indeed, all apes including humans possess relatively long arms, with the low intermembral index of humans being caused by the lengthening of the hindlimbs rather than the shortening of the forelimbs (Schultz, 1969). The high intermembral index of *Pan* again reflects the emphasis on suspensory locomotion (Zihlman, 1992). However, such information only goes so far towards under-

Fig. 3. Moment arms at the shoulder, elbow and wrist for Chimp 95. B(s): biceps (short head), B(l): biceps (long head), CB: coracobrachialis, LD: latissimus dorsi, TM: teres major, T(lo): Triceps (long head), B: biceps, T: triceps, BR: brachioradialis, BC: brachialis, WE: wrist extensors, WF: wrist flexors, ECRL: extensor carpi radialis longus, ECRB: extensor carpi radialis brevis, EDC: extensor digitorum communis, PL: palmaris longus, FDS: flexor digitorum superficialis, FDP: flexor

digitorum profundus, FCR: flexor carpi radialis, FCU: flexor carpi ulnaris. At the shoulder biceps (short head) and coracobrachialis inserted in the same place and were measured together, as were flexor digitorum superficialis and flexor digitorum profundus at the wrist. The wrist flexor moment arm at the elbow consists of FCU, FCR, and FDS which were measured together. The wrist extensor moment arm at the elbow consists of ECRL, ECRB, and EDC. These were also measured together.

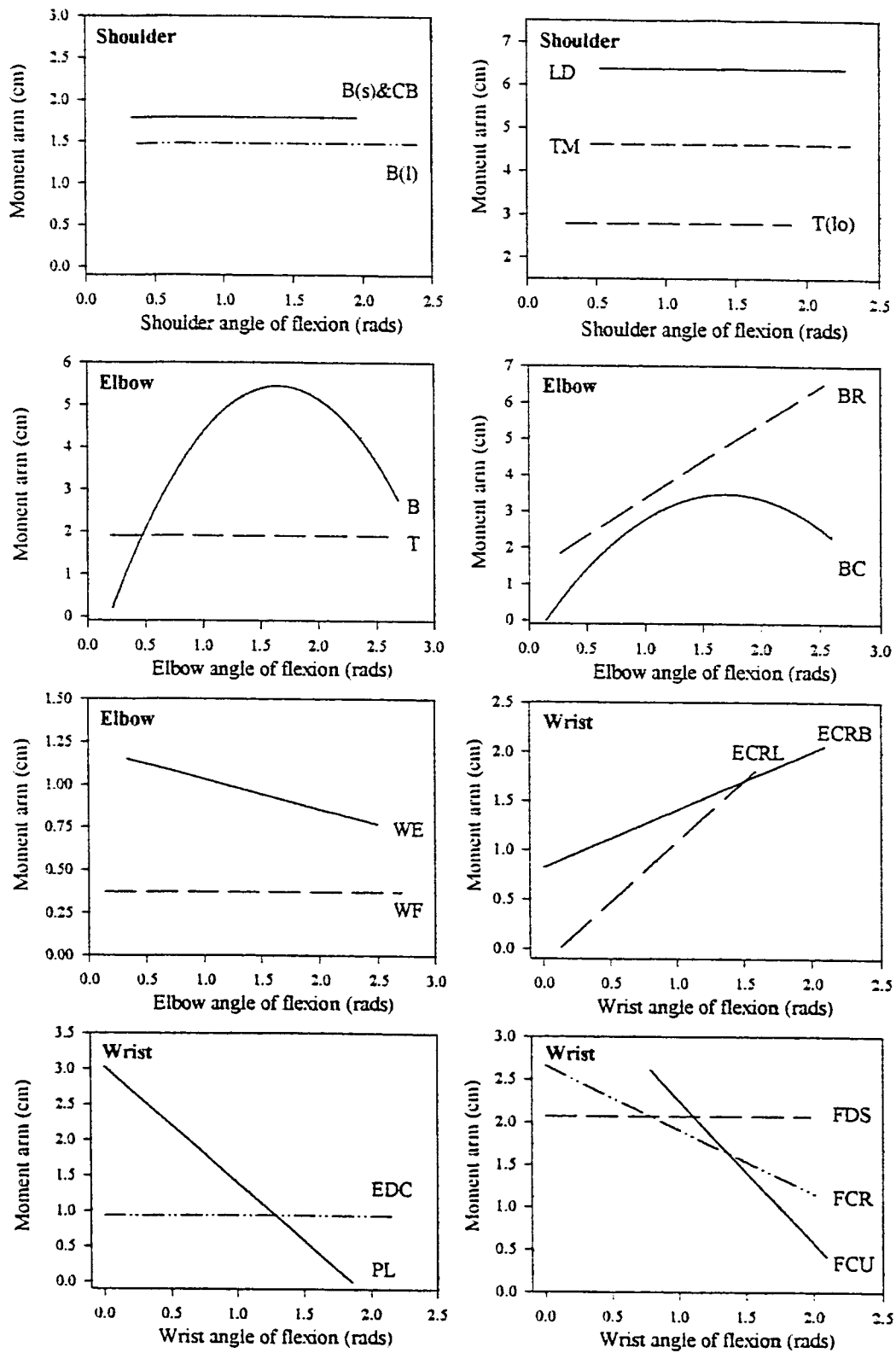


Fig. 3.

TABLE 14. Equations of best fit and r^2 values for moment arm (cm) regressions at the shoulder, elbow and wrist

Muscle	Equation of best fit	r^2 value
Biceps (elbow)	$0.33 - 1.46x + 4.18x^2 - 0.84x^3$	0.99
Brachialis (elbow)	$0.12 - 0.66x + 2.44x^2 - 0.48x^3$	0.99
Biceps (long head) (shoulder)	$-0.66 + 1.48x$	0.93
Brachioradialis (elbow)	$0.07 + 1.31x + 1.03x^2$	0.98
Biceps (short head) and coracobrachialis (shoulder)	$-0.53 + 1.79x$	0.98
E. carpi radialis brevis (wrist)	$2.92 - 0.82x - 0.30x^2$	0.99
E. carpi radialis longus (wrist)	$1.49 + 0.14x - 0.62x^2$	0.91
E. digitorum communis (wrist)	$2.20 - 0.94x$	0.94
F. carpi radialis (wrist)	$-0.07 + 2.66x - 0.38x^2$	0.99
F. carpi ulnaris (wrist)	$-2.62 + 3.93x - 0.84x^2$	0.99
F. digitorum superficialis (wrist)	$-0.05 + 2.07x$	0.95
Latissimus dorsi (shoulder)	$-4.20 + 6.38x$	0.99
Palmaris longus (wrist)	$0.07 + 3.03x - 0.82x^2$	0.99
Triceps (elbow)	$5.06 - 1.91x$	0.99
Triceps (long head) (shoulder)	$-0.82 + 2.79x$	0.98
Teres major (shoulder)	$-2.68 + 4.63x$	0.92
Wrist extensors (elbow)	$-0.42 + 1.21x - 0.09x^2$	0.99
Wrist flexors (elbow)	$0.25 + 0.37x$	0.89

x is the joint angle (rads).

TABLE 15. Mean muscle group moment arms (cm) for the forelimb*

	Chimpanzee		Human	
	Elbow	Wrist	Elbow	Wrist
Elbow flexors	3.70	—	4.54	—
Elbow extensors	2.10	—	1.39	—
Wrist flexors	0.41	2.04	0.74	1.27
Wrist extensors	1.17	0.94	1.09	0.52

*Calculated for a body mass of 50 kg, assuming geometric similarity. Unfortunately none of the studies from which moment arms were obtained provide the anthropomorphic data necessary to scale the human moment arm subjects to 50 kg. It is therefore assumed that the subjects used to obtain the moment arms were the same height and mass as the PCSA subjects. This may result in an error in the scaled values.

standing the relationship between anatomy and locomotion. Analyses of muscle dimensions can shed new light on this area.

Hindlimb muscle dimensions

The performance of a muscle is dictated by its force-velocity and force-length characteristics (Fukunaga et al., 1992; Wickiewicz et al., 1983, 1984; Brand et al., 1986). Tension production increases in proportion to the physiological cross-sectional area of a muscle, and velocity of shortening increases in proportion to fascicle length; the longer the fascicle, the faster is the potential velocity of shortening (Wickiewicz et al., 1983). In general, during everyday activities, muscles fascicles in vivo can shorten by up to 30% of their length at rest (Dimery, 1985). Long fascicles can produce larger angular movements about the joints than short fascicles,

while remaining within the range of sarcomere lengths at which large forces can be exerted (Rauwerdink, 1991). It is apparent from Table 6 that chimpanzees have significantly longer fascicles than humans for all hindlimb muscle groups, suggesting that chimpanzee hindlimbs are primarily designed to achieve the wide range of movement that observations of chimpanzees suggest is necessary for quadrumanous climbing. This result agrees with Rauwerdink's (1991, 1993) finding that climbing species tend to have longer fascicles than walking species. Muscle PCSAs are substantially larger in humans except for the deep hind flexors. This muscle group will be less important in human bipedalism because the toes do not need to be very mobile.

The fascicle lengths of different muscle groups within the hindlimb, in relation to each other, shows a similar pattern for both chimpanzees and humans. The adductors and the hamstrings have the longest fascicles followed by the quadriceps. However, in chimpanzees, the plantar flexors come next followed by the deep hind flexors, but in humans the plantar flexors have the shortest fascicles. This difference is related to the role of the Achilles tendon in humans. In chimpanzees, the muscles of the triceps surae are designed for mobility and large joint displacements (Rauwerdink, 1993; Preuschoft et al., 1992). In contrast, the plantar flexors in humans have to produce relatively

TABLE 16. Predicted and observed muscle group dimensions for Chimp 95*

	Muscle mass (kg)		Fascicle length (cm)		PCSA (cm ²)	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
Quadriceps	0.56	0.68	9.2	6.0	56.0	107.2
Adductors and hamstrings	0.95	1.05	18.9	11.4	47.5	86.7
Plantar flexors	0.29	0.31	6.6	3.7	40.5	79.4
Deep hind flexors	0.12	0.07	6.0	3.1	19.2	19.6

* Predicted values are based on allometric equations for primates from Alexander et al. (1981). The adductor and hamstring groups are combined to allow direct comparison with Alexander et al.'s (1981) data.

large forces, especially in bipedal running (De Vita, 1994; McCaw and De Vita, 1995). Consequently, the human Achilles tendon has evolved a role in storing elastic energy by tendon compliance (Ker et al., 1988; Alexander and Ker, 1990). In such cases, energy is saved by developing shorter fascicles and correspondingly longer tendons, both to decrease muscle mass and because tendons are less metabolically costly than are muscle fascicles (Dimery et al., 1986). The primary role for the muscle fascicles is therefore to maintain tension, for which short fascicles are mechanically adequate (Ker et al., 1988), hence the large PCSA for this muscle group (Table 6).

Alexander et al. (1981) analysed the allometric relationships between body mass and lower extremity muscle dimensions in a variety of mammals (including humans but not chimpanzees). They found that the distal leg muscles of primates tend to be large in comparison to other mammals, with long muscle fascicles as required for the mobility of their prehensile hands and feet. The present results agree with their conclusions. Table 16 compares our results to predicted values for the primate sample of Alexander et al. (1981) with predicted PCSAs calculated by substituting predicted mass and fascicle lengths into Eq. (1). We find that chimpanzees have longer fascicles in all muscles than are predicted for primates, but smaller muscle masses and PCSAs (with the exception of the deep hind flexors). However this is, at least in part, a reflection of Alexander et al.'s (1981) sample being biased by the use of humans as the sole representative of species with large body masses.

Hindlimb moment arms

Figure 2 presents the measured moment arms about the hip, knee, and ankle for the

major muscles of the leg. The difference in moment arm of the total quadriceps and the rectus femoris is due to a small proportion of the vasti fascicles inserting onto either side of the knee joint, thus limiting the movement of the quadriceps. These insertions determined the movement of the joint in the experiments, but in the living animal different fascicles within the vasti probably shorten to different extents (Lewis et al., 1988; Botinelli et al., 1991), keeping all the fascicles taut as the joint moves. We believe that the low apparent moment arm measured in the experiments with the quadriceps intact apply only to these few fascicles, and that the results of our experiments with the rectus femoris alone give the best estimate of the moment arm for the bulk of the muscle.

Yamazaki (1985) also made estimates of moment arms on a chimpanzee of similar age and mass by measuring the distance from the centre of rotation of the joint to the line of action of each muscle for a single, unspecified joint angle. Our results are reasonably consistent with Yamazaki's except for the quadriceps at the knee, for which he records a moment arm of 5.0 cm. It is likely that this value represents the moment arm of the rectus femoris at the knee. However, in the light of our results it still appears to be rather high.

Long muscle fascicles can produce larger angular movements at the joints than short muscle fascicles. However, their effect on joint angulation is also influenced by the moment arm of the muscle about the joint. The important quantity is the ratio of fascicle length/moment arm (Alexander, 1981, 1993). Large ratios indicate the ability to move joints through large angles. Table 17 provides this ratio for the major hindlimb muscles for chimpanzees and humans. It

TABLE 17. Ratios of muscles fascicle length to moment arm*

	Chimpanzee			Human		
	Hip	Knee	Ankle	Hip	Knee	Ankle
Quadriceps	2.5	4.1	—	1.1	1.4	—
Adductors	3.6	—	—	5.3	—	—
Hamstrings	3.4	5.3	—	1.3	2.8	—
Plantar flexors	—	4.9	2.0	—	2.1	0.5

*The quadriceps at the hip was calculated using rectus femoris fascicle lengths only and the plantar flexors at the knee using gastrocnemius fascicles.

shows clearly that, with the exception of the adductors at the hip, chimpanzees are adapted for considerably more movement at the joints than humans, as would be expected for prehensile limbs which must be able to exert forces in a wide range of positions. In contrast, as Alexander (1993) notes, human running requires large forces to be exerted with the limbs in particular positions, which are about the same in each stride.

Calculation of hindlimb joint moments of forces

The maximum isometric stress of vertebrate skeletal muscle is approximately 300 kN m^{-2} , although muscles acting eccentrically can exert far higher stresses (Wells, 1965; Narici et al., 1992; James et al., 1995). Using this value, it is possible to estimate the maximum mid-stance joint moments that chimpanzees can exert. Table 18 presents joint moments normalised by body mass and by leg length, which allows direct comparison between muscle groups calculated for chimpanzees and humans. Moments of force are calculated for joint angles exhibited at mid-stance in both species.

Chimpanzees stand bipedally with hips and knees significantly more flexed than occurs in humans. Consequently, to be able to exert equal maximum ground forces, chimpanzees would need muscles capable of exerting larger moments at the joints. The results in Table 18 indicate that this is not the case. In comparison to humans, chimpanzee muscles subject to the same stresses exert smaller moments at the joints, particularly in the quadriceps, at the knee, and the plantar flexors. This is because humans have far larger PCSAs and comparable mo-

ment arms for these muscle groups. This difference may be exaggerated by the likelihood that our chimpanzee muscle dimensions were not obtained from animals in peak health. The adductors at the hip are an exception. This result, combined with the reduced fascicle length/moment arm ratio for chimpanzee adductors in Table 17 suggest that their role in force production may be more important in chimpanzee locomotion than their role in mobility.

In reality, human muscles do not exert maximum isometric stress during bipedal walking, and as a result joint moments would be smaller than those presented here. In contrast, realistic stresses in chimpanzee bipedalism may reach maximum isometric stress, particularly in running. The faster a biped runs, the lower the duty factor and the higher the ground forces. Therefore, running performance is limited by the ability of muscles to exert large moments. A "bent-hip, bent-knee" (Stern and Susman, 1983) posture requires more muscle force than the relatively straight-legged run of humans, and would therefore require even greater moments and muscle stresses. It is also possible that at times stresses in the quadriceps will exceed maximum isometric stress, because they must act eccentrically to maintain a bipedal posture whilst the hamstrings flex the knee joint. This may explain why free-ranging chimpanzees have only been observed using bipedalism in short bursts, and are rarely observed running bipedally (Hunt, 1992; Doran, 1992a,b), which would require even larger moments at the joints.

Forelimb muscle dimensions

When human and chimpanzee muscle dimensions are scaled to 50 kg body mass (Table 12), it is apparent that the differences between them are much less pronounced than for the hindlimb anatomy. Nevertheless there are interesting results. In chimpanzees, the elbow and wrist flexors have the largest muscle masses in comparison to the extensor groups and all human muscle groups. However, the comparatively long fascicles of the elbow flexors in chimpanzees result in a PCSA comparable to that of the elbow extensors, which presumably reflects the need for large excursions and force pro-

TABLE 18. Calculation of moments of force at the hip (Mhip), knee (Mknee), and ankle (Mankle) for humans and chimpanzees assuming maximum isometric stress of 300 kN m^{-2} *

	Chimpanzee			Human		
	Mhip	Mknee	Mankle	Mhip	Mknee	Mankle
Quadriceps	0.55	1.93	—	1.01	6.24	—
Adductors	2.4	—	—	0.89	—	—
Hamstrings	1.28	1.04	—	3.05	1.63	—
Plantar flexors	—	0.48	2.07	—	0.92	7.79

* Moments (Nm) are divided by body mass (kg) \times leg length (m). Chimpanzee moment arms are as presented here except for the quadriceps at the knee which is taken as the moment arm for rectus femoris. Mid-stance joint angles for chimpanzees are from Okada (1985) and for humans, from our own video recordings.

duction at the elbow during climbing, since the range of joint positions required for terrestrial quadrupedalism is relatively small. In contrast, the PCSA of the human elbow extensors is considerably larger than that of the flexors.

Muscle PCSAs are larger in all chimpanzee than in human muscles. Clearly, this reflects the use of the forelimbs in chimpanzee but not human locomotion. Alexander (1974) has proposed that the dimensions of bones and muscles are to be understood largely in relation to the most strenuous activities in which they are used. Whilst terrestrial quadrupedalism accounts for 84% of chimpanzees daily locomotor repertoire (Doran, 1992b), it is climbing and arboreal locomotion which forms the most strenuous locomotor activities, due to the effects of gravity and the discontinuous and three-dimensional nature of the substrates, and it is thus likely that the increased force potential of chimpanzee forelimbs is related to climbing activities. The wrist flexors in chimpanzees possess the largest PCSA, which may reflect the importance of these muscles in gripping, manipulation, and other aspects of climbing. However, when the muscle masses are scaled on the basis of segment length (Table 13), the size difference between human and chimpanzee wrist flexors is removed. In both species, the wrist extensors are the smallest muscle group with comparable fascicle lengths and cross-sectional areas.

In the hindlimb, chimpanzees were found to possess substantially longer fascicles than humans due to the emphasis on force production in the human leg and mobility in the chimpanzee. A comparison of Tables 6 and 12 show that human forelimb fascicles are

generally longer than in the hindlimb, although, with the exception of the elbow flexors, they are only three-quarters the length of chimpanzee forelimb fascicles. Long fascicles are particularly important in chimpanzees because they need to be able to exert forces in a wide range of joint positions during arboreal locomotion. The length range in which a muscle can generate active force is proportional to fascicle length, and thus longer fascicles mean that the muscle can exert force over a wider range of joint angles. In arboreal climbing (and in terrestrial quadrupedalism), this applies equally to the fore- and hindlimbs, and therefore it is not surprising that chimpanzees have broadly similar sized muscles and fascicles in their legs and arms, although the fascicles of the adductors and hamstrings are outstandingly long.

Alexander et al. (1981) calculated allometric equations for the muscle masses and fascicle lengths of the triceps (elbow extensors) and foreflexors (wrist flexors) in a variety of primates (not human or chimpanzee) and other mammals. They concluded that primate foreflexors were larger and had longer fascicles than the other groups studied. This is because primates, in comparison to other quadrupedal mammals, tend to use their forelimbs in a more versatile fashion (Larson and Stern, 1986). Table 19 shows that, in both the elbow extensors and wrist flexors, chimpanzees have smaller PCSAs and longer fascicles than are predicted for primates as a whole, demonstrating that the need for mobility is even more dominant in chimpanzee limb anatomy than for most other primates.

TABLE 19. Predicted and observed muscle group dimensions for Chimp 95*

	Muscle mass (kg)		Fascicle length (cm)		PCSA (cm ²)	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
Elbow extensors	0.33	0.59	9.4	5.8	33.6	95.8
Wrist flexors	0.43	0.40	8.4	5.1	48.2	74.4

* Predicted values are based on allometric equations for primates from Alexander et al. (1981).

TABLE 20. Ratios of muscle fascicle length to moment arm

	Chimpanzee		Human	
	Elbow	Wrist	Elbow	Wrist
Elbow flexors	3.8	—	3.0	—
Elbow extensors	5.0	—	5.5	—
Wrist flexors	22.4	4.5	9.6	5.6
Wrist extensors	6.6	8.2	5.4	11.4

TABLE 21. Calculation of moments of force at the elbow (Melbow) and wrist (Mwrist) for humans and chimpanzees assuming maximum isometric stress of 300 kN m⁻² *

	Chimpanzee		Human	
	Melbow	Mwrist	Melbow	Mwrist
Elbow flexors	1.29	—	1.06	—
Elbow extensors	0.78	—	0.68	—
Wrist flexors	0.09	1.30	0.24	0.57
Wrist extensors	0.18	0.19	0.30	0.13

* Moments (Nm) are divided by body mass (kg) × arm length (m).

Forelimb moment arms

The results in Table 15 suggest that in general chimpanzees possess longer forelimb moment arms than do humans, except for the elbow flexors and the wrist flexors at the elbow which are slightly longer in humans. Table 20 provides the ratios of fascicle length/moment arm for chimpanzee and human muscles. Large ratios indicate the ability to move the joints through large angles (Alexander, 1993). Both species seem to have similar ranges of joint positions, except that the value for the wrist flexors at the elbow is remarkably high in chimpanzees, which means that wrist flexor fascicle length is affected very little by changes in elbow angle.

Calculation of forelimb joint moments of force

Table 21 compares chimpanzee and human joint moments calculated for the joint angles specified above, assuming maximum isometric stress, and normalised by body mass and arm length. The demands on the arms during quadrumanous climbing would lead us to expect that chimpanzees can exert greater moments at the elbow and wrist than can humans. The results in Table 21 support this hypothesis, although the differences between chimpanzee and human forelimbs are again not as pronounced as for the hindlimbs. Furthermore, the moments of force that human forelimbs are capable of exerting are substantially smaller than the hindlimbs. In chimpanzees, forelimb mo-

ments are slightly smaller than hindlimb moments of force (although note that chimpanzee arms are longer than their legs), which is in line with the concept of "hindlimb drive" (Kimura et al., 1979) in quadrupedal terrestrial locomotion.

CONCLUSION

In conclusion, when the effects of body mass are removed, all forelimb muscle masses, fascicle lengths, and PCSAs are smaller in humans than in chimpanzees, which clearly reflects the use of the forelimbs in chimpanzee, but not human, locomotion. The wrist flexors of chimpanzees in particular are more designed for force production and moment generation than in humans. Chimpanzee arms and legs are generally similar, except that the hindlimbs can produce slightly larger joint moments. Human forelimbs have a considerably larger range of movement, but less capacity for force production, than their hindlimbs.

Chimpanzee hindlimbs were found to possess longer fascicles in all muscles but smaller PCSAs than are predicted for primates as a whole and for hypothetical 50 kg humans. This suggests that the emphasis is on joint mobility at the expense of tension production in chimpanzee locomotion. For terrestrial locomotion, this allows longer stride length, and for arboreal climbing, it increases the distances which can be bridged,

but both are achieved at the expense of the forces which can be delivered by the hindlimb. The deep hind flexors are the only muscle group in chimpanzees that have a comparable PCSA to humans, which reflects the relative unimportance of these muscles in habitual bipedalism but greater role in climbing to produce force and sustain mobility at the joints. Moment arms differ in that chimpanzee adductors have large moment arms at the hip, and human quadriceps have large moment arms at the knee.

In comparison to humans, chimpanzee muscles subject to the same stresses exert far smaller moments at the joints, particularly in the quadriceps and plantar flexors. These differences in muscle architecture and function suggest that humans are primarily adapted for running because they are capable of exerting large moments at the joints, but their short muscle fascicles limit mobility. In contrast, chimpanzees have retained generalised primate adaptations for climbing whilst their small hindlimb muscle PCSAs will restrict their ability to run bipedally.

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